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Geographical ecology of dry forest tree communities in the West Indies

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Abstract

Aim: Seasonally dry tropical forest (SDTF) of the Caribbean Islands (primarily West Indies) is floristically distinct from Neotropical SDTF in Central and South America. We evaluate whether tree species composition was associated with climatic gradients or geographical distance. Turnover (dissimilarity) in species composition of different islands or among more distant sites would suggest communities structured by

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speciation and dispersal limitations. A nested pattern would be consistent with a steep resource gradient. Correlation of species composition with climatic variation would suggest communities structured by broad-scale environmental filtering.

Location: The West Indies (The Bahamas, Cuba, Hispaniola, Jamaica, Puerto Rico, US Virgin Islands, Guadeloupe, Martinique, St. Lucia), Providencia (Colombia), south Florida (USA) and Florida Keys (USA).

Taxon: Seed plants—woody taxa (primarily trees).

Methods: We compiled 572 plots from 23 surveys conducted between 1969 and 2016. Hierarchical clustering of species in plots, and indicator species analysis for the resulting groups of sites, identified geographical patterns of turnover in species composition. Nonparametric analysis of variance, applied to principal components of bioclimatic variables, determined the degree of covariation in climate with location. Nestedness versus turnover in species composition was evaluated using beta diversity partitioning. Generalized dissimilarity modelling partitioned the effect of climate versus geographical distance on species composition.

Results: Despite a set of commonly occurring species, SDTF tree community composition was distinct among islands and was characterized by spatial turnover on climatic gradients that covaried with geographical gradients. Greater Antillean islands were characterized by endemic indicator species. Northern subtropical areas supported distinct, rather than nested, SDTF communities in spite of low levels of endemism.

Main conclusions: The SDTF species composition was correlated with climatic variation. SDTF on large Greater Antillean islands (Hispaniola, Jamaica and Cuba) was characterized by endemic species, consistent with their geological history and the biogeography of plant lineages. These results suggest that both environmental filtering and speciation shape Caribbean SDTF tree communities.

KEYWORDS
beta diversity, Caribbean, community composition, seasonally dry tropical forest, species turnover, tropical dry forest, West Indies

1 | INTRODUCTION

The West Indies, the islands of the Caribbean Basin, share a fascinating geological and biogeographical history that has resulted in complex distributions of terrestrial organisms (Iturralde-Vinent & MacPhee, 1999; Santiago-Valentin & Olmstead, 2004). These islands constitute a global biodiversity hotspot (Maunder et al., 2008), and have experienced major prehistoric (e.g. Steadman et al., 2005, 2015) and historic (Dixon, Hamilton, Pagiola, & Segnestam, 2001) human impacts on that biodiversity. Terrestrial plant communities in the West Indies include most major tropical habitats, from mangrove to cloud forest (Dinerstein et al., 1995). The West Indian terrestrial vegetation comprises a seed plant flora with 71% endemism (Acevedo-Rodríguez & Strong, 2008, 2012), a value that increases to 77% for woody species in its dry forests (DRYFLOR et al., 2016).

We focus on seasonally dry tropical forest (SDTF), also known as tropical dry forest. SDTF has been called the most threatened tropical forest community, both globally (Gillespie et al., 2012; Miles et al., 2006) and in the West Indies (Banda-R, Weintritt, & Pennington, 2016), owing to its history of extensive human disturbance (Murphy & Lugo, 1986). We define SDTF as closed-canopy tropical and subtropical forests typically found in frost-free areas characterized by low and seasonal availability of moisture, where annual rainfall is less than ca. 1800 mm with a 3–6-month dry season receiving <100 mm per month (Lugo, Medina, Trejo-Torres, & Helmer, 2006). SDTF is distinguished from tropical savanna by its closed tree canopy and lack of fire, and from tropical rain forest, with which it shares few species, by its deciduous to semi-deciduous canopy, shorter stature, and lesser vertical complexity. SDTF is often found on fertile soils, and in the West Indies it is usually found at low elevation on the lee side of mountainous islands or in coastal zones (DRYFLOR et al., 2016).

The tree flora of the SDTF biome in the Neotropics has a shared evolutionary and biogeographical history (Dexter et al., 2015). In a

recent study evaluating SDTF diversity across the entire Neotropics, the West Indian ("Antillean") subregion was identified as floristically distinct (DRYFLOR et al., 2016). Subregional patterns have previously been identified in continental Neotropical SDTF (Neves, Dexter, Pennington, Bueno, & Oliveira Filho, 2015). A better understanding of variation in SDTF species composition and its drivers within the West Indies may further identify floristically distinct subregions—patterns of diversity useful for understanding biogeographical processes and setting regional conservation targets.

An analysis of SDTF tree species composition in just three Caribbean archipelagos (Bahamas, Puerto Rico, US Virgin Islands) suggested similarity in dominant species composition across that portion of the West Indies in spite of the differences in geological history (Franklin, Ripplinger, Marcano-Vega, Freid, & Steadman, 2015), leaving open the question of whether SDTF shows distinct subregional composition within the islands of the Caribbean Basin. Using data compiled from almost 600 forest inventory plots or relevés, recording over 650 woody plant taxa from 11 countries (22 individual islands) across the West Indies, we addressed the following research questions:

1. What are the patterns of tree species composition in Caribbean SDTF?

We expected that composition would be the least distinctive (would consist of a nested subset of species found elsewhere) in low elevation areas, young islands and areas at the climatic margins of the tropics (northern Bahamas, Florida), and most distinctive (greater species turnover among locations) in geologically old and complex, large islands of the Greater Antilles where 30–50% of plant species are island endemics. Nestedness is expected when there is a steep gradient in resource supply with strong environmental filtering at one end of the gradient (Chase & Leibold, 2003) and has also been attributed to dispersal limitations in archipelagos (Lomolino, 1996). Alternatively, a non-nested pattern dominated by turnover in species composition among all sites across space would occur if dispersal limitation, as well as speciation, was important and therefore the "local" (subregional) species pool contributed strongly to the community. This integrated time-area effect, with larger, older areas having accumulated more species (Fine & Ree, 2006), could be manifested as distinct SDTF composition in the three subregions with different geological histories (Greater Antilles, Lesser Antilles, Bahamian Archipelago).

2. How much variation in species composition among sites (species turnover across space) is related to geographical distance among sites, environmental gradients (Austin, 1985), or both?

Ecological communities are assembled from a regional species pool through the processes of speciation, biotic and abiotic filtering (selection), and dispersal (Vellend, 2010; Zobel, 1997). We expected variation to be related to geographical distance if community composition has been strongly affected by dispersal limitations and speciation (island endemism) (e.g. Gillespie et al., 2013; Ibanez et al., 2018; Pennington, Lavin, & Oliveira-Filho, 2009), especially within large, old islands in the Greater Antilles. Alternatively, the amount of environmental variation across the study region suggests that compositional variation may also be related to environmental filtering (Franklin et al., 2013; Toledo et al., 2012). If there is environmental filtering of a region-wide species pool, for example, for species that can tolerate a strong dry season (Markesteijn, Poorter, Bongers, Paz, & Sack, 2011), and poor dispersal has not been a factor limiting distributions, then species composition would be weakly structured by geographical distance. Here, we pursue both research questions by synthesizing data from 23 studies of SDTF throughout the West Indies.

2 | MATERIALS AND METHODS

2.1 | Study area and species composition data

Caribbean SDTF occurs most often on limestone (carbonate) substrates. From a tectonic perspective, Cuba and the Bahamian Archipelago lie on the North American plate, whereas all other sampled islands lie on the Caribbean plate, which is moving eastward relative to the adjoining North and South American plates (Meschede & Frisch, 1998). The Puerto Rico Archipelago and the Virgin Islands are found on the same microplate that moves somewhat independently (Hippolyte, Mann, & Grindlay, 2005) and they share biogeographical affinities (Acevedo-Rodríguez & Strong, 2008). Complex interactions during the Cenozoic (mostly large-scale strike-slip faulting) at both the northern and southern boundaries of the Caribbean plate have deformed the diverse bedrock formations on the Greater Antillean islands (Cuba, Hispaniola, Jamaica and Puerto Rico + Virgin Islands, Keppie, 2014). In contrast, the Bahamian islands and southern Florida are tectonically stable, geologically very young and consist exclusively of carbonate bedrock (Mylroie & Mylroie, 2013; Randazzo & Jones, 1997). The Lesser Antillean island arc, represented in our dataset by Guadeloupe, Martinique and St. Lucia, is the result of late Cenozoic subduction of Atlantic Ocean crust at the eastern margin of the Caribbean plate (Meschede & Frisch, 1998).

Species occurrences or abundances within sampled locations (sites) were compiled from 23 published and unpublished datasets (Table 1; Supporting Information Appendix S1 Table S1) spanning 11 regions—islands or archipelagos—across the West Indies (Figure 1a). One region is continental—the south Florida peninsula—but we will refer to islands or archipelagos for simplicity. We include data from Florida (USA) and Providencia (Colombia) because, although not considered biogeographically part of the West Indies (Acevedo-Rodríguez & Strong, 2012), they represent the northern and western limits of STDF in the Caribbean Basin and allow us to build a region-wide understanding of species composition. Furthermore, south Florida and the Keys are part of the Caribbean Biodiversity Hotspot (Maunder et al., 2008). Sites were located from 13° to 26° N and 61° to 85° W. Elevations ranged from sea level to 884 m and median site elevation was 38 m.

TABLE 1 Summary of community composition data sources for woody taxa in Caribbean Seasonally Dry Tropical Forest (STDF)

Region	Archipelago	Island/Location	# stems ≥5 cm	Sites	Citation
Bahamian Archipelago	Bahamas	Abaco, Eleuthera	4220	42	(Franklin et al., 2015)
Bahamian Archipelago	Bahamas	N. Andros	3203	12	(I. K. Smith & Vankat, 1992)
Bahamian Archipelago	Bahamas	Cat, Eleuthera, San Salvador	6061	71	(Daniels, 2016)
Bahamian Archipelago	Bahamas	Crooked Island	1739	17	J. Franklin, unpublished
Greater Antilles	Cuba	Dry forest	sXp 1339	31	(Borhidi, 1991)
Greater Antilles	Hispaniola	Los Haitises	105	1	Gentry plot (mobot.org)
Greater Antilles	Hispaniola	Sierra Martin Garcia	sXp 1130	35	(García et al., 2007)
Greater Antilles	Hispaniola	Sierra Martin Garcia	644	11	J. Franklin, unpublished
Greater Antilles	Jamaica	Bossue	27	2	D. Kelly, unpublished
Greater Antilles	Jamaica	Broom Hall, Round Hill	1257	4	(Kelly et al., 1988)
Greater Antilles	Jamaica	Hellshire Hills	684	12	(McLaren, McDonald, Hall, & Healey, 2005)
Greater Antilles	Puerto Rico	Mona Island	310	8	(Rojas-Sandoval et al., 2014)
Greater Antilles	Puerto Rico	Mona Island	sXp 660	46	(Melendez-Ackerman et al., 2016)
Greater Antilles	Puerto Rico	Northeast Puerto Rico	306	3	(Gould, González, & Carrero Rivera, 2006)
Greater Antilles	Puerto Rico	Dry forest	1369	113	FIA; (Franklin et al., 2015)
Lesser Antilles	Guadeloupe	Grand-Terre	642	6	(Imbert & Portecop, 2008)
Lesser Antilles	Martinique	Martinique	257	16	(Vennetier, 2015)
Lesser Antilles	St Lucia	St Lucia	826	21	(Gonzalez & Zak, 1996)
Lesser Antilles	US Virgin Islands	Dry forest	1077	90	FIA; (Franklin et al., 2015)
South Florida and Keys	Florida	Florida Keys	1773	9	(Ross, O'Brien, & Flynn, 1992)
South Florida and Keys	Florida	Key Largo, Florida Keys	1632	23	(Ross, Carrington, Flynn, & Ruiz, 2001)
South Florida and Keys	Florida	South Florida and Keys	2995	23	(Gillespie, 2005)
SW Caribbean	San Andrés, Providencia and Santa Catalina	Providencia	1155	60	(J. Ruiz et al., 2005)

Sites correspond to the number of sites used in the present study. # stems ≥5 cm is the number of tree stems ≥5 cm diameter at a standard height (1.3–1.45 m) included in the present study. sXp indicated species in plot abundance or presence data (rather than individual stem measurements). FIA = data from US Forest Service Forest Inventory and Analysis (Gray et al., 2012; O'Connell et al., 2014). For more details see Table S1.

Data were from ecological surveys or forest inventories between 1969 and 2016, and most consisted of stem diameter measurements at a standard height (1.3–1.45 m) for woody or arboreal taxa of seed plants identified to species level (in a very few cases to morphospecies, genus or family) in fixed-area plots. For multi-stemmed individuals, all stems above the diameter threshold were measured and each stem was treated as an observation in our study. Two studies recorded cover or Braun-Blanquet importance values for different height strata, and one recorded species presence/absence (Table 1). Plot size ranged from 28 to 1000 m^2, with most falling between 100 and 500 m^2. In total, measurements of almost 46,000 stems and 3,000 species-in-sites (abundance or occurrence) were compiled, and then stem diameter data were filtered to about 35,000 individuals ≥5 cm (corresponding to the largest minimum diameter in all but one of the datasets; Table S1, Table 1). While we refer to tree species for simplicity in this paper, the data include palms (Arecaceae), arboreal cacti (Cactaceae) and woody taxa typically taking a shrubby form if they had at least one stem ≥5 cm in diameter.

Multivariate analyses were conducted using both species relative abundance (Importance Value calculated from averaging relative basal area and relative stem density, or from cover or Braun-Blanquet values) and the presence/absence. The results were very similar and so we emphasize results based on the presence/absence, allowing an additional dataset from Hispaniola and a total of 637 sites to be potentially included for the analysis. After sites with zero compositional Jaccard distance were eliminated (required for multivariate ordination based on a dissimilarity matrix), 572 sites remained. Most (54) of the eliminated sites were monospecific plots from the large US Forest Service's Forest Inventory and Analysis (FIA) (Gray, Brandeis, Shaw, McWilliams, & Miles, 2012) dataset for Puerto Rico and the US Virgin Islands, and their removal helped to improve the evenness of sampling across the region.

Most data were collected during the last two decades and their site locations were recorded using a hand-held global positioning system (GPS) in the field (Table S1). For datasets acquired in earlier decades, geographical coordinates were assigned from site maps and descriptions using Google Earth (Table S1). Our environmental variables consist primarily of 1-km resolution climate data that are spatially autocorrelated over long distances. For the Cuba data, only a general description of the sample location was given and these have

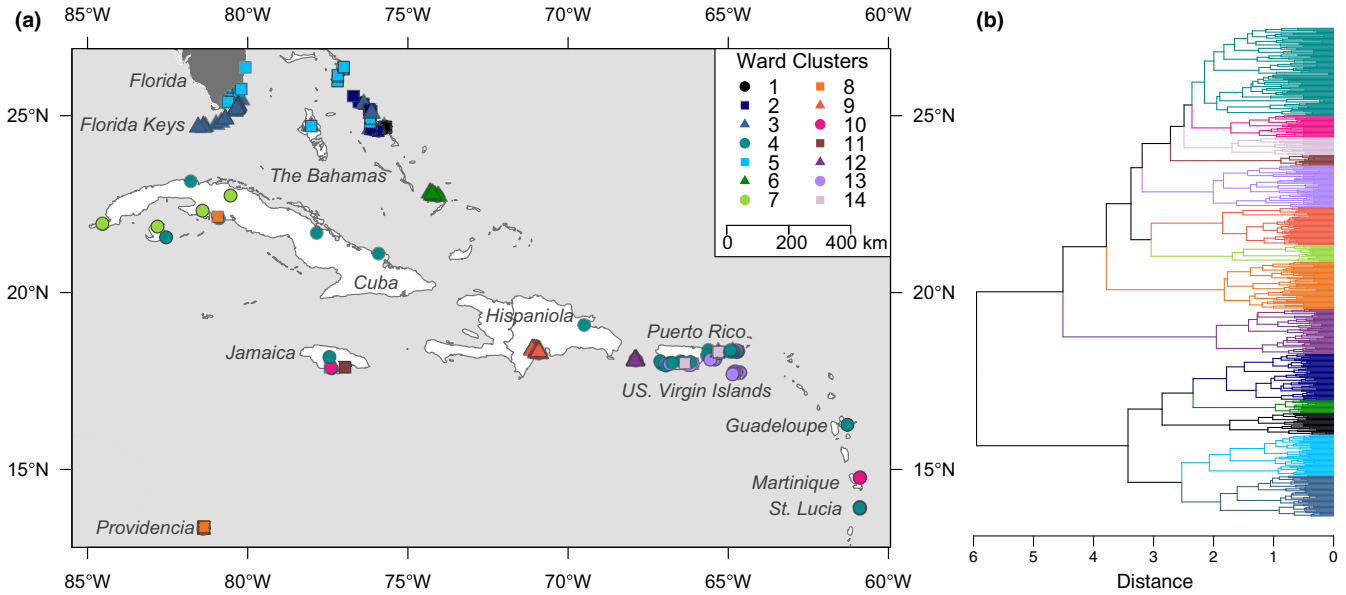

FIGURE 1 a) Map of site locations showing group membership and b) cluster dendrogram resulting from Ward's hierarchical clustering of Jaccard distance matrix among 554 sites based on the species presence/absence showing relationships among groups (using the same colour scheme for group as in (a)). Note that in (a), at this map scale individual sites are not always visible and one symbol may represent tens of nearby sites (see Tables 1 and S2)

the lowest precision (we estimate 10 km), introducing some noise to the analysis.

2.2 | Environmental data

Bioclimatic ("Bioclim") variables (Nix & Busby, 1986) at 1-km spatial resolution were acquired from worldclim.org (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). These data only cover terrestrial areas and thus excluded the small island of Providencia, where we calculated bioclimatic variables (one value for all sites) using local climate records that featured average but not maximum and minimum monthly temperatures (Jorge Ruiz & Molano-González, 2017).

The 19 bioclimatic variables provided by worldclim.org describe seasonal and annual averages of precipitation and averages and extremes of temperature based on long-term means of monthly values. They tend to be correlated, and a subset was initially selected based on their relevance to SDTF distribution (DRYFLOR et al., 2016; Murphy & Lugo, 1986) and our ability to calculate them for Providencia. We selected annual mean temperature and precipitation, mean temperature of the warmest and coldest quarters, temperature seasonality and precipitation of the wettest and driest months (Table 2). These were further examined for multicollinearity, which led to precipitation of the wettest month being eliminated from some analyses (Table 2).

Elevation values were extracted from NASA's Shuttle Radar Topography Mission (STRM) 90-m resolution data. Elevation is considered an indirect gradient (Austin, 2002), strongly related to temperature (via the lapse rate), and precipitation (orography), but we included it because it can serve as a proxy for finer scale climate variation than is available from the Bioclim 1-km data.

2.3 | Analyses

Hierarchical agglomerative clustering using Jaccard distance and Ward's linkage (Peet & Roberts, 2013) was applied to species presence/absence data for 572 sites and 649 taxa to identify patterns of tree species composition in Caribbean SDTF (question 1). Differences among clusters were tested using analysis of variance based on 999 permutations (PERMANOVA, Anderson, 2001). Patterns of similarities and differences among groups identified by clustering, and their distribution with respect to environmental gradients, were visualized using indirect ordination based on non-metric multidimensional scaling (NMDS, Clarke, 1993). Indicator species analysis (Dufrêne & Legendre, 1997) identified species characteristic of the groups of sites identified by hierarchical clustering. The multivariate vegetation analyses used are robust to variations in forest plot sizes ranging from 50 to 1000 m^2 (Otypková & Chytry, 2006), encompassing most of the range found in this study. We were able to use Importance Value (IV) and stem density (from the plots where those were measured) to evaluate patterns of species frequency versus abundance within and among groups defined in the multivariate analyses.

The degree of correlation between climate predictor variables and geographical coordinates was calculated. Principal components analysis was applied to the bioclimatic variables for the sites and then analysis of variance was used to evaluate whether climatic differences were due to sites belonging to different islands/archipelagos. Beta diversity (compositional dissimilarity among sites) was partitioned into nested and turnover components (question 1) using the R package 'betapart' (Baselga & Orme, 2012). We assessed the importance of climate versus geographical distances between sites

TABLE 2 Bioclimatic and geographical variables analysed and their ranges of values for the 572 West Indian sites analysed

Abbreviation (bio)	Variable	Range
MAT (bio1)*	Annual Mean Temperature	21.0–27.4°C
CV_T (bio4)*	Temperature Seasonality (Coefficient of Variation)	7.8–33.1
Twarm (bio10)*	Mean Temperature of Warmest Quarter	22.1–28.6°C
Tcold (bio11)*	Mean Temperature of Coldest Quarter	19.2–25.0°C
MAP (bio12)*	Annual Precipitation	164–2026 mm
Pwet (bio13)	Precipitation of Wettest Period (month)	33–336 mm
Pdry (bio14)*	Precipitation of Driest Period (month)	2–98 mm
alt	'Altitude' (elevation above sea level)	0–884 m
lat	Latitude	13.3° to 26.4°N
long	Longitude	60.9° to 84.5°W

bio# is the Bioclim variable name (used in worldclim.org).
*Predictors used in generalized dissimilarity modelling (GDM). Bioclimatic variables were from worldclim.org. Elevation from NASA Shuttle Radar Topography Mission (STRM) 90 m data downloaded using the getData() function in the R package raster. Latitude and longitude were from GPS data recorded for each site or, if not available, approximated using methods described in Table S1.

in explaining dissimilarity in species composition (question 2) using generalized dissimilarity modelling (GDM, Ferrier, Manion, Elith, & Richardson, 2007) applied to the same Jaccard community distance matrix (appropriate for beta diversity studies, Legendre & Cáceres, 2013) used in our clustering and ordination analyses. A reduced set of bioclimatic predictors (Table 2) was used; because elevation represents an indirect gradient, and precipitation of the wettest month (Pwet, bio13) was correlated with mean annual precipitation (MAP, bio12; $r = .89$), we dropped these two variables from the GDM. GDM was implemented using the R package "gdm" (Manion, Lisk, Ferrier, Nieto-Lugilde, & Fitzpatrick, 2016). We compared the variance explained by different models computed with both climate and geographical distance as predictors versus models with only climate or only geographical distances as predictors (Legendre, 2008). The importance of each variable in driving compositional dissimilarity was calculated from the curves produced by GDM (functions showing how beta diversity varies with each environmental and geographical predictor while holding all other variables constant) by summing the coefficients of the partial regressions (Fitzpatrick et al., 2013).

Analyses (clustering, NMDS, analysis of variance, GDM, variance partitioning) were repeated aggregating taxa to the genus level as a first-order approximation of the functional, rather than taxonomic, similarity of sites, assuming that plant species in the same genus share similar traits and ecological requirements, and play similar roles in the community. Detrended correspondence analysis (DCA, Hill & Gauch, 1980), a form of indirect ordination, was also performed for both species and genus data in order to compare their relative amount of turnover (compositional dissimilarity) in terms of ordination axis length (in units of standard deviation of species turnover). We expected that less turnover of genera would reflect greater functional similarity of TDF throughout the West Indies as compared to the species-level analysis which reflects more local patterns of speciation and endemism. Multivariate community analyses were performed using the R packages 'vegan' (Oksanen et al., 2011) and labdsv (Roberts, 2012). All analyses were done using R 3.3.3 (R Core Team, 2017) (script provided in Supporting Information Appendix S2).

3 | RESULTS

3.1 | Biogeography of community composition

Clustering based on Jaccard distance calculated from the presence/absence of species, cut at a multivariate Ward's distance of 2, yielded 14 groups of sites (Figure 1b) that were significantly different ($R^2 = .41$; $F = 29.9$; $p = .001$). Clusters consisted primarily of sites within archipelagos or nearby archipelagos (Figure 1; Figure 2 vs. 3; Table S2), although some clusters overlapped (Fig. S1). The most distinct was cluster 8 (most sites from Providencia). Island/archipelago explained 30% of the variation in the community distance matrix (PERMANOVA; $F = 24.2$, $p = .001$).

The SDTF in the West Indies is characterized by several species-rich plant families including Fabaceae, Myrtaceae (see also Acevedo-Rodríguez & Strong, 2012), Polygonaceae, Rhamnaceae and Sapindaceae (Table 3). Indicator species analysis (Table 3; Table S3) revealed the following patterns: Northern Caribbean groups 1, 2 (Cat, Eleuthera, and San Salvador islands), and 6 (Crooked Island) are clusters of Bahamian sites characterized by *Coccothrinax argentata*, *Vachellia choriophylla* and *Bursera inaguensis* respectively. Northern Caribbean group 3 (Florida Keys and Bahamas) has *Piscidia piscipula*, *Metopium toxiferum* and *Coccoloba diversifolia* as indicator species, while group 5 (Abaco, Andros and Eleuthera in the Bahamas, Florida peninsula, Florida Keys, Jamaica) is characterized by *Exothea paniculata*, *Sideroxylon salicifolium* and *Lysiloma sambicu*. Indicator species for Northern Caribbean groups include few endemics (Table S3).

Group 4 includes 102 sites from throughout the region (47 from Puerto Rico but others from Cuba, Guadeloupe, Jamaica, Providencia, Crooked Island) with *Maytenus laevigata* and *Pictetia aculeata* (West Indian endemics) as characteristic species, although neither Indicator Values nor *p*-values are strong (i.e. not >.1 or <.01 respectively) for species associated with this group (Tables 3, S3). Lesser Antillean group 10 (Martinique, St. Lucia, with a few sites from the Greater Antilles) had Lesser Antillean (*Tabebuia pallida*) and West Indian (*Coccoloba pubescens*) endemics as indicator species. Group 8 includes 53 of 58 sites from Providencia (and two sites from the Greater Antilles), with *Vachellia collinsii* and *Campomanesia* sp. as indicators.

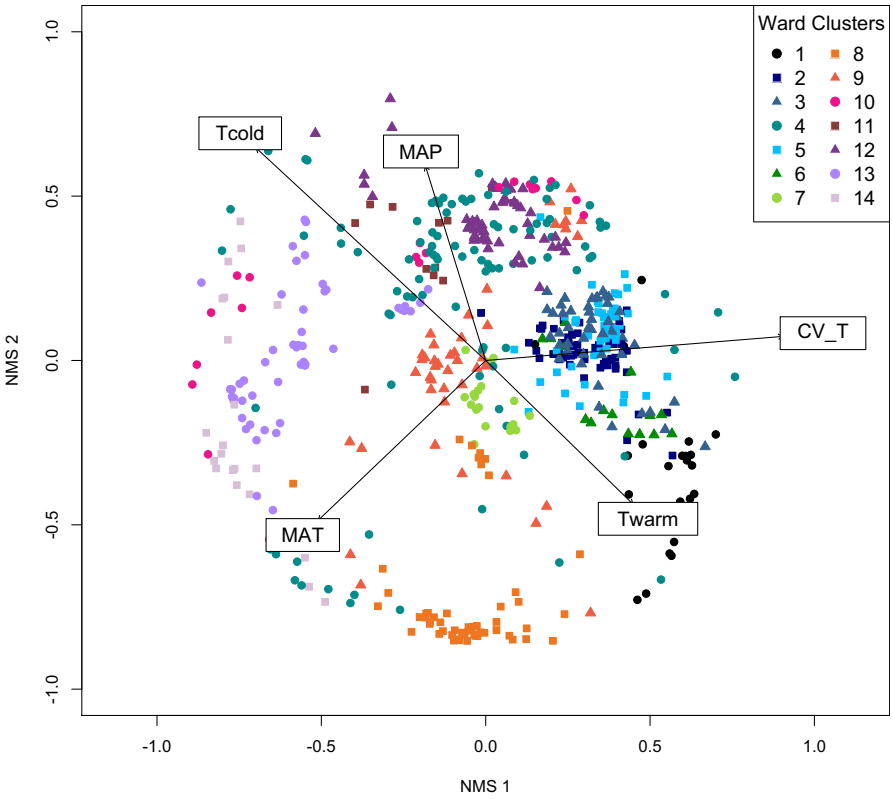

FIGURE 2 Sites arrayed in two dimensions based on indirect ordination, non-metric multidimensional scaling (NMDS), applied to a Jaccard distance matrix calculated from the presence/absence of species in sites, labelled by cluster number (clustered using Ward's distance). Vector length indicates degree of correlation of environmental variables with ordination axes (bioclimatic and geographical abbreviations as in Table 2)

Large Greater Antillean islands tend to be distinctive in their composition. Group 7 includes 20 of the 30 sites from Cuba, group 11 includes 12 of the 16 sites from Jamaica, and Group 9 includes 44 of 46 sites from Hispaniola, each characterized by many high indicator value species, including endemics (Table 3; Table S3). Group 12 comprises sites from Mona (in the Puerto Rico Archipelago) and the main island of Puerto Rico with *Coccoloba microstachya* and other West Indian endemics as indicators. Two groups (13, 14) that characterize "novel ecosystems" sampled mainly in Puerto Rico and the US Virgin Islands (Table S2), were dominated by non-native and invasive tree species—*Leucaena leucocephala* (Wolfe & Van Bloem, 2012) and *Melicoccus bijugatus* in group 13, and *Vachellia farnesiana* and *Prosopis pallida* in group 14.

Twelve of the 20 most frequently recorded native species occurred in eight or more of the 14 groups (Table S4). Dry forest specialist *Bursera simaruba* was the most widespread species, and was often abundant (as measured by IV or stem density) or even dominant in sites where it was recorded (see also Lugo et al., 2006). *Bourreria baccata*, *Krugiodendron ferreum*, *Amyris elemifera* and *Eugenia axillaris* also were widespread and moderately abundant (occurring in 9–12 groups, 17–26% of sites, with 0.01–0.09 average IV). *Coccoloba diversifolia*, *Metopium toxiferum*, *Swietenia mahagoni* and *Lysiloma latisiliquum* were moderately widespread and abundant (7–8 groups, 11–20% of sites, 0.09–0.16 IV; Table S4).

At the genus level (298 taxa in 569 sites), there was less overall turnover and greater overlap among sites from different islands or archipelagos. For example, a detrended correspondence analysis (DCA) based on species data had greater eigenvalues and axis lengths (in units of standard deviation of species turnover) than a DCA of genera. DCA axis 1 length for species data was 7.6, while for genus data it was 3.9 (eigenvalues 0.71 and 0.42 respectively). In GDM there was less total variance explained in the genus-level distance matrix (34%) than at the species level (40%), and less overlap of climate and geographical distance (27% for species, 14% for genera). The general pattern of proportions variance explained by environment versus geographical space is similar– 10% climate, 1% geographical distance, 14% combined at the genus level. At the aggregated taxonomic level, however, the Lesser Antillean sites (St. Lucia, Martinique) clustered with those from Puerto Rico and USVI, and from other Greater Antillean islands (Table S5). Also, the Northern Caribbean clusters were more central to the ordination, sharing many genera with the other groups (Fig. S2).

Almost all variation in site environmental data (bioclimatic variables and elevation, Table 2) was explained by archipelago membership (999 permutations; $R^2 = .95$; $F = 1082$; $p = .001$). Higher latitude Florida and Bahamas have greater temperature seasonality, higher average temperature of the warmest quarter, and lower average temperature of the coolest quarter. Lower latitude Providencia and St. Lucia have higher mean annual temperature and lower mean annual precipitation. Easterly (less negative) longitude Puerto Rico and the US Virgin Islands have higher average temperature of the coldest quarter, lower temperature of the warmest quarter and lower temperature seasonality. Hispaniola, Puerto Rico and US Virgin

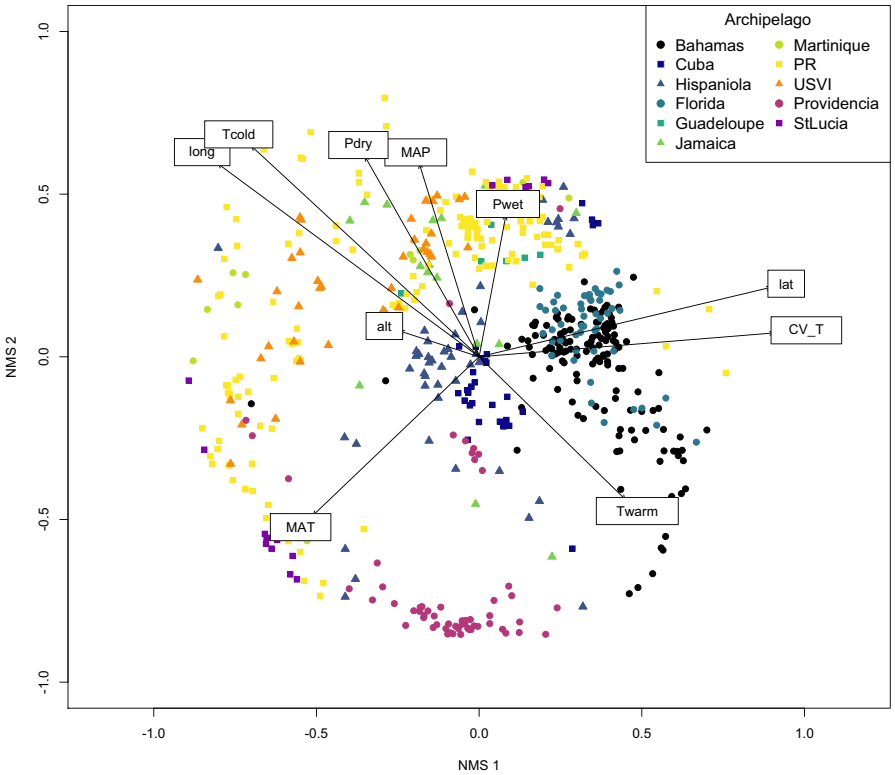

FIGURE 3 Sites arrayed in two dimensions based on indirect ordination, non-metric multidimensional scaling (NMDS), applied to a Jaccard distance matrix calculated from the presence/absence of species in sites, labelled by archipelago. Vectors indicate correlation of environmental (bioclimatic and geographical abbreviations as in Table 2) variables with ordination axes. PR = Puerto Rico. USVI = US Virgin Islands elevation

Islands include higher elevation SDTF sites (Figure 3; Fig. S3), the highest being 884 m on the leeward side of Sierra Martín Garcia, Dominican Republic.

3.2 | Geographical and bioclimatic gradients

Essentially all variance in the compositional dissimilarity matrix was attributed to species turnover among sites (99.6%) rather than nested patterns of species composition in sites (Jaccard dissimilarity based on the presence/absence) by beta partitioning. Most explained variance in the dissimilarity matrix was explained by climatic dissimilarity (12%), or shared geographical distance and climate (27%) and very little by distance alone (1%; Figure 4). Climate was strongly geographically structured (Figure 3, Fig. S3). Precipitation of the driest month and average temperature of the coldest quarter were the climate variables most important in explaining variance in the dissimilarity matrix (Table 4).

4 | DISCUSSION

A recent study of SDTF throughout the Western Hemisphere placed Caribbean (Antillean) SDTF as distinct from dry forest in the continental Neotropics, characterized by a high proportion of endemic tree species (DRYFLOR et al., 2016). We have further demonstrated intraregional patterns of species composition in West Indian dry forests, characterized by species turnover among archipelagos and islands (e.g. Franklin et al., 2013; Ibanez et al., 2018). Turnover is correlated with climatic variation, which in turn is strongly geographically structured (T. W. Smith & Lundholm, 2010) such that most variation in climate is explained by archipelago.

Climate and climate + distance accounted for most of the (explained) variance in site compositional dissimilarity. A strong climate signal would be expected if comparing wet and seasonally dry tropical forests in the region, as has been shown globally (Guan et al., 2015). However, our study, like Neves et al. (2015), identified climate variation associated with SDTF variation within a Neotropical subregion. Inter-site geographical distance explains very little additional variance. In other words, nearby SDTF sites on well-sampled islands could be quite dissimilar owing to fine-scale environmental heterogeneity. Spatial vegetation heterogeneity is not uncommon in water-stressed environments including SDTF (Gerhardt & Hytteborn, 1992), especially in karstic settings (Zhang, Hu, & Hu, 2014). Within our study region, for example, on Mona island the abundance of tree species is associated with fine-scale soil nutrient variation (Melendez-Ackerman et al., 2016). Furthermore, there are functional physiological differences among species that are associated with soil conditions including available moisture (Medina, Cuevas, Marcano-Vega, Meléndez-Ackerman, & Helmer, 2017).

While we found very little effect of distance alone on composition, suggesting that dispersal limitation is not important in shaping SDTF composition, species composition differed among archipelagos, a pattern that could be consistent with dispersal limitation (Franklin et al., 2013). We are not able to completely isolate climate versus distance effects in our study given the strongly geographically structured climate.

TABLE 3 Indicator taxa for 14 vegetation groups in the West Indies established by clustering, and islands. Top five species with indicator values (IV) >0.5 or, if none >0.5, the top three values are shown

Cluster	Islands	Species (Family)	IV	Probability
1	Cat, Eleuthera, San Salvador (Bahamas)	*Coccothrinax argentata* (Arecaceae)	0.47	0.001
		*Casuarina equisetifolia** (Casuarinaceae)	0.35	0.001
		Sabal palmetto (Arecaceae)	0.17	0.001
2	Cat, Eleuthera, San Salvador (Bahamas)	*Vachellia choriophylla* [W] (Fabaceae)	0.37	0.001
		Reynosia septentrionalis (Rhamnaceae)	0.24	0.001
3	Florida Keys, Eleuthera, Andros, Cat (Bahamas)	*Piscidia piscipula* (Fabaceae)	0.42	0.001
		Metopium toxiferum (Anacardiaceae)	0.24	0.001
		Coccoloba diversifolia (Polygonaceae)	0.22	0.001
4	Puerto Rico; USVI; Cuba; Guadeloupe; Jamaica; Providencia; Crooked (Bahamas)	*Maytenus laevigata* [W] (Celastraceae)	0.09	0.009
		Pictetia aculeata [GA] (Fabaceae)	0.05	0.042
		Myrciaria floribunda (Myrtaceae)	0.05	0.042
5	Abaco, Andros, Eleuthera (Bahamas); Florida; Florida Keys; Jamaica	*Exothea paniculata* (Sapindaceae)	0.34	0.001
		Sideroxylon salicifolium (Sapotaceae)	0.25	0.001
		Lysiloma sabicu (Fabaceae)	0.21	0.001
		Myrsine floridana (Primulaceae)	0.05	0.042
6	Crooked (Bahamas)	*Bursera inaguensis* [W] (Burseraceae)	0.91	0.001
		Guapira obtusata (Nyctaginaceae)	0.52	0.001
		Thouinia discolor [B] (Sapindaceae)	0.51	0.001
7	Cuba	*Oxandra lanceolata* [GA] (Annonaceae)	0.89	0.001
		Zuelania guidonia (Salicaceae)	0.84	0.001
		Cecropia peltata (Urticaceae)	0.77	0.001
		Amyris balsamifera (Rutaceae)	0.77	0.001
		Cedrela odorata (Meliaceae)	0.77	0.001
8	Providencia; Puerto Rico; Cuba	*Vachellia collinsii* (Fabaceae)	0.71	0.001
		Campomanesia sp. (Myrtaceae)	0.40	0.001
		Euphorbia cotinifolia (Euphorbiaceae)	0.36	0.001
9	Hispaniola	*Senna atomaria* (Fabaceae)	0.66	0.001
		Pilosocereus polygonus (Cactaceae)	0.57	0.001
		Guaiacum officinale (Zygophyllaceae)	0.49	0.001
10	Martinique; St. Lucia; Jamaica	*Tabebuia pallida* [LA] (Bignoniaceae)	0.52	0.001
		Coccoloba pubescens [W] (Polygonaceae)	0.42	0.001
		Lonchocarpus punctatus (Fabaceae)	0.18	0.001
11	Jamaica	*Comocladia velutina* [J] (Anacardiaceae)	1.00	0.001
		Linociera sp. (Oleaceae)	0.98	0.001
		Bauhinia divaricata [H] (Fabaceae)	0.76	0.001
		Casearia sylvestris (Salicaceae)	0.76	0.001
		Sarcomphalus laurinus [J] (Rhamnaceae)	0.74	0.001
12	Mona, Puerto Rico	*Coccoloba microstachya* [W] (Polygonaceae)	0.69	0.001
		Reynosia uncinata [W] (Rhamnaceae)	0.46	0.001
		Stenostomum acutatum [W] (Rubiaceae)	0.35	0.001
13	Puerto Rico; USVI; Mona; Providencia	*Leucaena leucocephala** (Fabaceae)	0.29	0.001
		Trema micrantha (Cannabaceae)	0.09	0.01
		*Melicoccus bijugatus** (Sapindaceae)	0.08	0.01
14	Puerto Rico; USVI	*Vachellia farnesiana** (Fabaceae)	0.50	0.001
		*Prosopis pallida** (Fabaceae)	0.34	0.001
		Pithecellobium dulce (Fabaceae)	0.17	0.001

Endemic to [B] = Bahamas; [C] = Cuba; [GA] = Greater Antilles; [H] = Hispaniola; [LA] = Lesser Antilles; [P] = Puerto Rican Bank; [J] = Jamaica; [W] = West Indies; * = non-native, USVI = U.S. Virgin Islands.

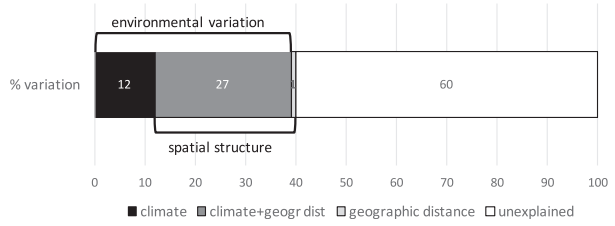

FIGURE 4 Proportion of variance (% variation) in compositional dissimilarity between sites (turnover or beta diversity) explained by climate variables, geographical distance (1%), their shared variation (27%), and unexplained variation, based on generalized dissimilarity modelling (GDM) of Jaccard distance matrix from presence/absence data

Floristic distinctions within the West Indies are enhanced by endemism in the three largest islands. One third to one half of the seed plant species found there are endemic to Jamaica (32%), Hispaniola (42%) and Cuba (51%), compared to the Lesser Antilles (14%), Puerto Rico and the Virgin Islands (14%), and the Bahamian Archipelago (9%) (Acevedo-Rodríguez & Strong, 2012). These patterns are reflected in the tree communities of the SDTF where we found similarities between the Bahamas and Florida, between the Puerto Rican Bank (Puerto Rico + Virgin Islands) and the Lesser Antilles, and even between these northern and southeastern subregions (see also Franklin et al., 2015). The most distinctive floristic expressions of SDTF, characterized by endemic indicator species, were found on Hispaniola, Jamaica and Cuba. Providencia, far from the other sampled islands, also supported distinct SDTF, although, as previously shown, it has greater floristic affinities with the West Indies than with Central America (J. Ruiz & Fandiño, 2010; J. Ruiz, Fandiño, & Chazdon, 2005).

The subregional patterns found in this study are consistent with the geological and biogeographical history of the West Indies. Much of the current Greater Antilles has been continuously above water since the Middle Eocene (Iturralde-Vinent & MacPhee, 1999), and so is much older than the Lesser Antilles and the Bahamian Archipelago. The Greater Antilles share part of their biogeographical history with southern Mexico and Central America where cooling and drying may have begun to shape modern plant communities in the Miocene and Pliocene (reviewed in Santiago-Valentin & Olmstead, 2004). Indeed, Pliocene climatic changes are thought to have shaped the biogeography and distribution of SDTF plants throughout the Neotropics (Linares-Palomino, Oliveira-Filho, & Pennington, 2011).

Biogeographical patterns based on plant phylogenies suggest that many West Indian lineages have origins in Mexico and Central America, whereas others originated within the Caribbean region (Santiago-Valentin & Olmstead, 2004). Overwater dispersal played an important role in interchanges of plant taxa both between the continents and among other land masses in the Caribbean Basin (Pennington & Dick, 2010), predating the late Pliocene Central American isthmian connection (O'Dea et al., 2016). Contemporary West Indian (Antillean) dry forests also share the greatest number of species with dry forests in Mexico and Central America/northern South America (DRYFLOR et al., 2016; Linares-Palomino et al., 2011). When analysed at a higher taxonomic level, we found Lesser Antillean SDTF to be similar to Greater Antillean, reflecting that the Lesser Antilles are geologically young (lack of genus-level endemism) and that their flora is largely Antillean rather than South American in origin (Acevedo-Rodríguez & Strong, 2012).

Contrary to our first prediction, we did not find that subtropical northern Bahamas and Florida supported a depauperate (nested) subset of Caribbean SDTF diversity. This is in contrast to nested patterns found over smaller spatial extents in response to habitat fragmentation (Ross, Sah, Ruiz, Spitzig, & Subedi, 2016). While the Bahamian archipelago is geologically young and does not support high levels of seed plant endemism (Acevedo-Rodríguez & Strong, 2012), we found that SDTF composition in this northern subregion is distinct within the Caribbean Basin (Franklin et al., 2015), consistent with the climatic differences found there (Figure 3; Fig. S3). West Indian SDTF tree species that characterize this subregion may be widely distributed but are not typical (indicators) of other subregions (Table 3), suggesting environmental sorting on the climatic gradient represented in our study (e.g. Table S3).

The high species turnover found in this study is driven by the many less common species that are important within and restricted to archipelagos or subregions. In contrast to broader scale Neotropical patterns (DRYFLOR et al., 2016), however, some widespread species also are found frequently (in many sites) and across many archipelagos or groups in the West Indies. These widespread "generalist" species may be those that are best adapted to recover from hurricane disturbance by coppicing, withstand seasonal drought and/or tolerate edaphic extremes (Murphy & Lugo, 1986; Rojas-Sandoval et al., 2014; Van Bloem, Murphy, & Lugo, 2003).

Future work is needed to better understand the effects of both natural and human disturbance on patterns of Caribbean SDTF composition. Hurricanes are an important natural disturbance in the Caribbean (Mumby, Vitolo, & Stephenson, 2011) driving forest dynamics (Gannon & Martin, 2014; Tanner, Rodriguez-Sanchez, Healey, Holdaway, & Bellingham, 2014), whereas continental Neotropical SDTF experiences fewer hurricanes on average (Bullock, Mooney, & Medina, 1995). Human disturbance includes forest clearing (Chazdon, 2014) and selective tree removal (Murphy & Lugo, 1986). Prehistorically and historically, humans have greatly reduced populations of

TABLE 4 Predictor variable relative importance (Importance) in generalized dissimilarity model (GDM) based on Jaccard distance matrix from species-in-sites presence/absence data. Variables as in Table 2

Environmental variables	Importance
Precipitation of Driest Period (Pdry)	0.14
Mean Temperature of Coldest Quarter (Tcold)	0.09
Mean Temperature of Warmest Quarter (Twarm)	0.05
Annual Mean Temperature (MAT)	0.03
Annual Precipitation (MAP)	0.03
Geographical (lat/long)	0.03
Temperature Seasonality (CV_T)	0.02

birds and other vertebrate dispersers of SDTF seeds on islands (e.g. Steadman, 2006; Steadman et al., 2005). In contrast with continental SDTF where wind dispersal of seeds is common (Bullock, 1995; Pennington, Prado, & Pendry, 2000), bird dispersal dominates Caribbean SDTF (Ray & Brown, 1994). Disturbance history is undoubtedly an important factor affecting site composition in our study but knowledge of the disturbance history of sites included in our study was very uneven among datasets and therefore, we could not directly analyse disturbance as factor. We did identify some West Indian SDTF tree communities that were dominated by non-native and invasive species (see also Franklin et al., 2015).

Low similarity and high turnover across space in this study suggest that conservation areas should range across West Indian countries and subregions in order to protect SDTF diversity (DRYFLOR et al., 2016). Our study provides unprecedented detail on the biogeography of woody SDTF species in the West Indies, supporting conservation and restoration decision-making in the region, but also highlighting data gaps. At the 2013 Caribbean Foresters Meeting, the National Forests Inventories Working Group noted that their most recent forest inventories were over 20 years old, and some Caribbean islands have never conducted a national forest inventory (Marcano-Vega et al., 2016). SDTF in the West Indies is in a critical state (Banda-R et al., 2016) and there is an urgent need for regionally coordinated forest inventories and monitoring.

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DATA ACCESSIBILITY

In support of reproducible science, the aggregated species presence/absence in sites, species list and environment by site data used in this study are deposited in the University of California—Riverside DASH repository (https://doi.org/10.6086/d1zh32).

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BIOSKETCH

Janet Franklin is a biogeographer who uses geospatial data and spatial analytical tools to study the past, present and future distributions of biodiversity and ecosystems in relation to the physical environment, evolutionary and ecological processes, and human impacts, focusing on patterns and dynamics of terrestrial plant communities.

Author contributions: J.F. initiated the research and wrote the manuscript; J.F., R.A. and J.R. compiled and analysed the data; all other authors are experts on seasonally dry tropical forest in the Caribbean and provided data and contributed to the study design, interpretation of results and manuscript writing.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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